第46卷 第3期
2008年7月

古脊椎动物学报
VERTEBRATA PALASIATICA

pp.161－170
figs.1－5

云南昭通早泥盆世肉鳍鱼类一新属[1)]

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摘要：记述了产于云南昭通早泥盆世布拉格期基干肺鱼形动物一新属、新种——多孔弓鱼（*Arquatichthys porosus* gen. et sp. nov.）。新材料包括一件较为完整的下颌和鳞片若干。与基干肺鱼形动物相近的特征有：第四下齿骨水平凹线呈“L”形；下颌表面可见许多不规则排列的感觉管开孔；具三块冠状骨；冠状骨侧部为宽阔的小齿带；侧联合齿骨附着区较小；颌收肌窝大；菱形鳞片具明显的前腹突。鉴别特征包括下颌背缘明显隆起，以及后缘具加长的被覆压区。多孔弓鱼的发现为探讨肉鳍鱼类的早期分化提供了新的资料，在早期肉鳍鱼类的系统发育关系框架下讨论了鳞片的特征演化序列。

关键词：云南，早泥盆世，基干肺鱼形动物，鳞片演化
中图法分类号：Q915.862 **文献标识码**：A **文章编号**：1000－3118(2008)03－0161－10

AN EARLY DEVONIAN (PRAGIAN) SARCOPTERYGIAN FROM ZHAOTONG, YUNNAN, CHINA

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Abstract A new basal dipnomorph sarcopterygian, *Arquatichthys porosus* gen. et sp. nov., from the Lower Devonian (Pragian) of northeastern Yunnan, China, is described on the basis of a nearly complete mandible and several isolated scales. It closely resembles basal dipnomorphs in following characters: short and L-shaped pit-line of infradentary 4 (uniquely shared with dipnomorphs), small parasymphysial dental plate attachment, three coronoids, broad “tooth pavement” on the lateral portion of coronoids, large adductor fossa, irregularly scattered pores of mandibular sensory canal on the lateral surface of mandible, and distinct anteroventral process of rhomboid scale. *Arquatichthys* has a unique mandible morphology characterized by a strongly arched upper margin, and an elongated overlapped area by quadratojugal and maxillary. As the second dipnomorph from the Pragian of China, *Arquatichthys* adds evidences to understanding the early diversification of sarcopterygians. The character transitions of scales are discussed within the framework of the interrelationships of early sarcopterygians.
Key words Yunnan, Early Devonian, basal dipnomorph, scale character transitions

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1）国家重点基础研究发展规划项目（编号：2006CB806400），国家自然科学基金重点项目（编号：40332017），国家基础科学人才培养基金特殊学科点项目（编号：J0630965）和中国科学院知识创新工程青年人才领域前沿项目（编号：KJ207409）资助。

收稿日期：2007－11－27

1 Introduction

The Dipnomorpha includes two major lineages (Porolepiformes and Dipnoi), and some basal taxa such as *Powichthys* and *Youngolepis* (Ahlberg, 1991; Cloutier and Ahlberg, 1996; Janvier, 1996).

The Porolepiformes, an exclusively Devonian group, is characterized by the otic part of main lateral line canal passing through the center of postparietal, and by dendrodont teeth (Janvier, 1996). It has been divided into two families, Porolepididae and Holoptychiidae (Clément, 2001). Four of the best known representatives of the group are the Early Devonian porolepid *Porolepis* (Jarvik, 1942, 1950, 1972, 1980; Kulcyzcki, 1960) and the Middle to Late Devonian holoptychiids *Glyptolepis* (Jarvik, 1950, 1972, 1980), *Quebecius* (Schultze, 1973), and *Holoptychius* (Jarvik, 1942, 1950, 1972, 1980).

Powichthys and *Youngolepis* are from the Early Devonian (Lochkovian-Pragian) of Arctic Canada (*P. thorsteinssoni*), Spitsbergen (*P. spitsbergensis*), South China and Vietnam (*Youngolepis*). *Powichthys* displays a mixed suite of basal and advanced sarcopterygian features, and is known from two species: *P. thorsteinssoni* and *P. spitsbergensis* (Jessen, 1975, 1980; Clément and Janvier, 2004). It was referred to porolepiforms on the basis of its ethmoid region features (Jessen, 1975; Jarvik, 1980). However, the recent phylogenetic work shows that *Powichthys* is not a porolepiform (Ahlberg, 1991; Chang and Smith, 1992; Cloutier and Ahlberg, 1996; Zhu and Schultze, 1997; Zhu and Yu, 2002; Chang, 2004) although it shares many similarities with porolepiforms. *Youngolepis*, as the earliest known dipnomorph, occurred from the early Lochkovian to Pragian (Zhu and Zhao, 2006). It is quite similar to *Powichthys* and shares many features with "osteolepiforms" and porolepiforms (Chang and Yu, 1981; Chang, 1991; Chang and Smith, 1992). *Powichthys* and *Youngolepis* show transitional features between Porolepiformes and Dipnoi. However, the interrelationship of *Powichthys*, *Youngolepis* and Porolepiformes is still not fully resolved (Ahlberg, 1991; Cloutier and Ahlberg, 1996; Chang and Yu, 1997; Forey, 1998; Zhu et al., 1999, 2001; Zhu and Yu, 2002).

Arquatichthys porosus gen. et sp. nov., the second dipnomorph from the Pragian of China, shares many features with *Youngolepis*, *Powichthys*, porolepiforms and basal tetrapodomorphs. Its discovery provides new insights into the evolution of basal dipnomorphs and adds evidences to the understanding of the early diversification of sarcopterygians (Zhu and Zhao, 2006).

2 Geological setting

The materials were found from a yellow sandstone layer of the Posongchong Formation near Qingmen village, Zhaotong district, Yunnan. This fish-bearing horizon was first named as "Cuifengshan Formation", by comparison to the type locality of this formation in Qujing district, Yunnan (Xian and Zhou, 1978; Yun, 1978; Zhao, 1978). Liao et al. (1978) proposed that it would be more appropriate to name the horizon as the Posongchong Formation, considering the same lithology and fauna as the Posongchong Formation in Wenshan district, Yunnan. We adopt this suggestion in this paper. The fossils are distributed in the whole Qingmen section, in which two main outcrops have yielded abundant fish specimens (Fig. 1). The age of the Posongchong Formation is considered to be late Pragian, mainly based on the correlation of marine invertebrates and conodonts from the overlying Pojiao Formation (Hao et al., 2004). Four galeaspids (*Sanquiaspis zhaotongensis* Liu, 1975; *Qingmenaspis microculus* Pan and Wang, 1981; *Zhaotongaspis janvieri* Wang and Zhu, 1994; *Lungmenshanaspis yunnanensis* Wang et al., 1996), antiarchs, petalichthyids, onychodontids (Zhu and Janvier, 1994), as well as lingulids and plant remains, were reported from this site.

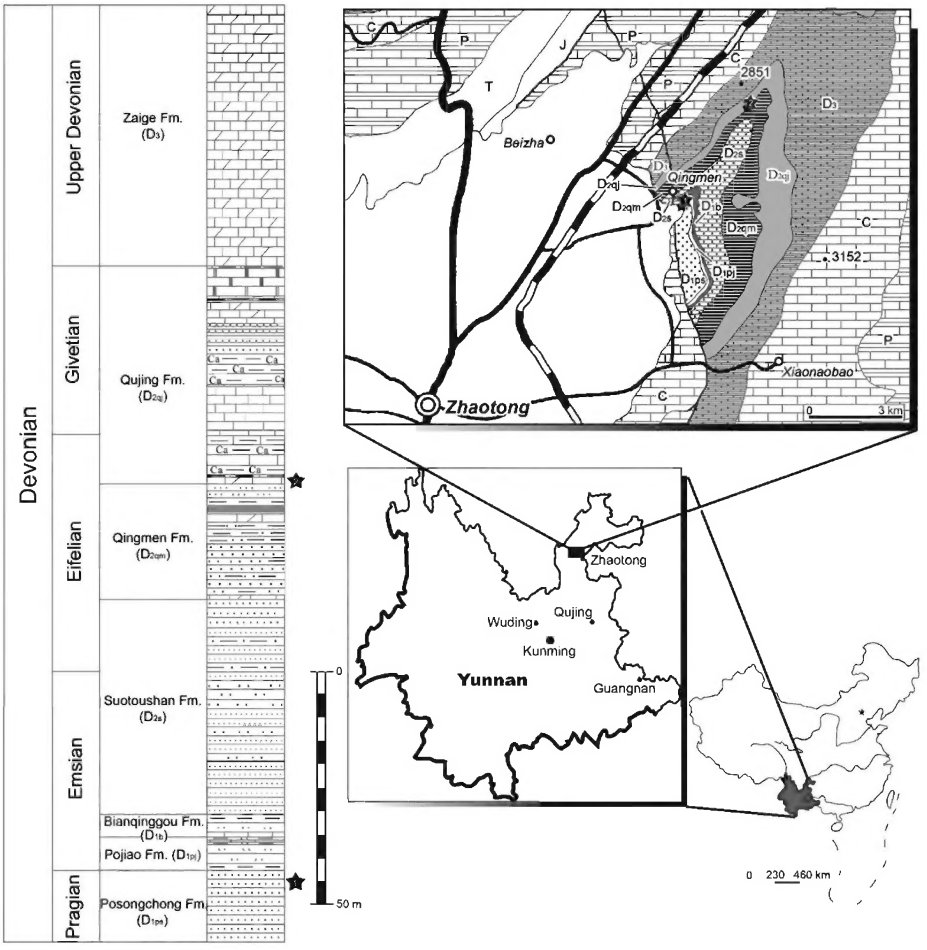

Fig. 1　Geographic location and stratigraphic positions of the fish sites (indicated by stars) in Zhaotong district, Yunnan Province, China

★ indicates the Early Devonian fish site, where *Arquatichthys porosus* gen. et sp. nov. was found;
★ indicates the Middle Devonian fish site

3　Systematic paleontology

Subclass Sarcopterygii Romer, 1955
Superdivision Dipnomorpha Ahlberg, 1991
***Arquatichthys porosus* gen. et sp. nov.**
(Figs. 2-4)

Etymology　Generic name referring to the strongly arched mandible (L. *arquata*, arched; Gk. *ichthys*, fish). The specific name is from Latin *porous*, in reference to irregularly scattered pores of sensory canal on the mandible surface.

Diagnosis　A sarcopterygian with a strongly arched upper margin of mandible, an elongated overlapped area by quadratojugal and maxillary on the mandible, abundant pores for branchings of the mandibular sensory canal, a strong anteroventral process on the scale, and the

cosmine surface of scale bearing 1-3 parallel striations along anterior margin.

Holotype Right mandible (IVPP V 15644).

Referred specimens Several detached scales (IVPP V 15645-15648).

Locality and horizon Zhaotong, northeastern Yunnan, China, Early Devonian (late Pragian), Posongchong Formation.

Description Mandible: The mandible is nearly complete with anterior part of the dentary tooth margin missing. Its posterior extremity is broken, but as judged from the preservation of the glenoid fossa, the missing part might be very short. The mandible agrees well with those of *Youngolepis*, *Powichthys*, porolepiforms and "osteolepiforms" in overall structure and shape.

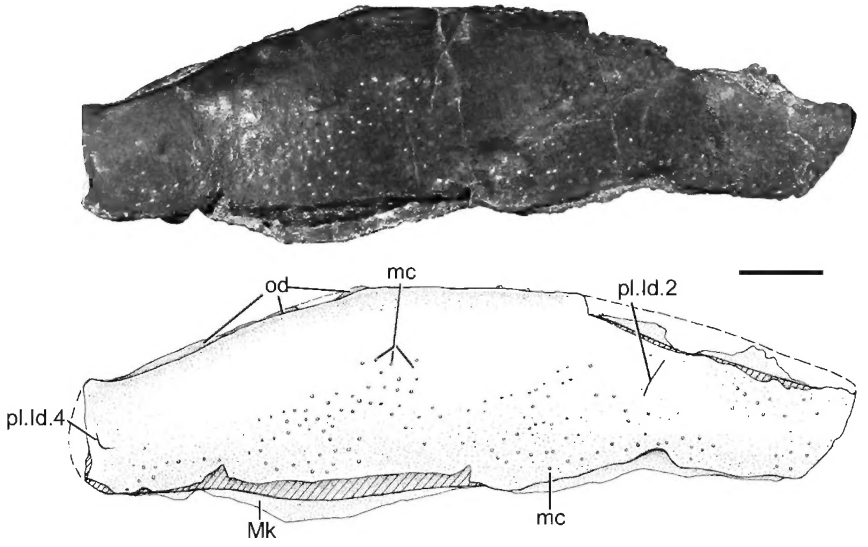

Fig. 2 The mandible of *Arquatichthys porosus* gen. et sp. nov. from Posongchong Formation, Lower Devonian, South China (holotype, IVPP V 15644) in dorsal view

Abbreviations: mc. pores of mandibular sensory canal; Mk. Meckelian bone; od. area of mandible overlapped by quadratojugal and maxillary; pl. Id. 2. pit-line of infradentary 2; pl. Id. 4. pit-line of infradentary 4 scale bar = 5 mm

The lateral side of the mandible has a continuous cover of cosmine, concealing the sutures between external dermal bones (dentary and infradentaries) (Fig. 2). The upper margin of the mandible is strongly arched, making the mandible relatively high, with the length about 3.6 times its height (this ratio in *Youngolepis* and *Kenichthys* is about 4). A marked long depressed area devoid of cosmine is on the posterodorsal margin of the mandible. This area, overlapped in its posterior part by the quadratojugal and in its anterior part by the maxillary, is extending forward to about the midway of the mandible. The mandibular sensory canal traverses the row of infradentaries, parallel to the long axis of the mandible. Numerous additional pores adjacent to the main sensory canal line appear to mark branches of this canal. The same condition can be observed in Porolepiformes (*Porolepis*, *Nasogaluakus*, *Quebecius* and *Glyptolepis*) (Jarvik, 1972; Cloutier and Schultze, 1996; Schultze, 2000), and some "osteolepids" (such as *Lativus* Jarvik, 1948). In *Powichthys*, though the pores of sensory canal are irregularly scattered on the skull roof, only a single row of sensory canal openings is present in the mandible (Jessen, 1980). The pit-line of infradentary 4 is L-shaped, and no horizontal pit-line is visible. This arrangement is quite different from that in tetrapodomorphs, in which the horizontal pit-line usually continues to the pit-line of infradentary 4. The L-shaped pit-line of infradentary 4 is also present

in Porolepiformes, *Powichthys* and *Youngolepis*. No infradentary foramen is visible in *Arquatichthys*. By comparison, these foramina are present in *Youngolepis*, *Powichthys*, porolepiforms (*Holoptychius*, *Laccognathus*, *Quebecius* and *Glyptolepis* occasionally) (Jarvik, 1972, 1980; Vorobyeva, 1980; Jessen, 1980; Chang, 1991; Cloutier and Schultze, 1996) and basal sarcopterygians (*Psarolepis*, *Achoania*, and *Styloichthys*) (Yu, 1998; Zhu and Yu, 2004). Posteriorly, the lower margin is partly damaged, and a flange extending beyond the ventral border of infradentaries can be seen laterally. This flange is conspicuous in *Styloichthys*, contributed by the Meckelian bone and the prearticular (Zhu and Yu, 2002; Friedman, 2007).

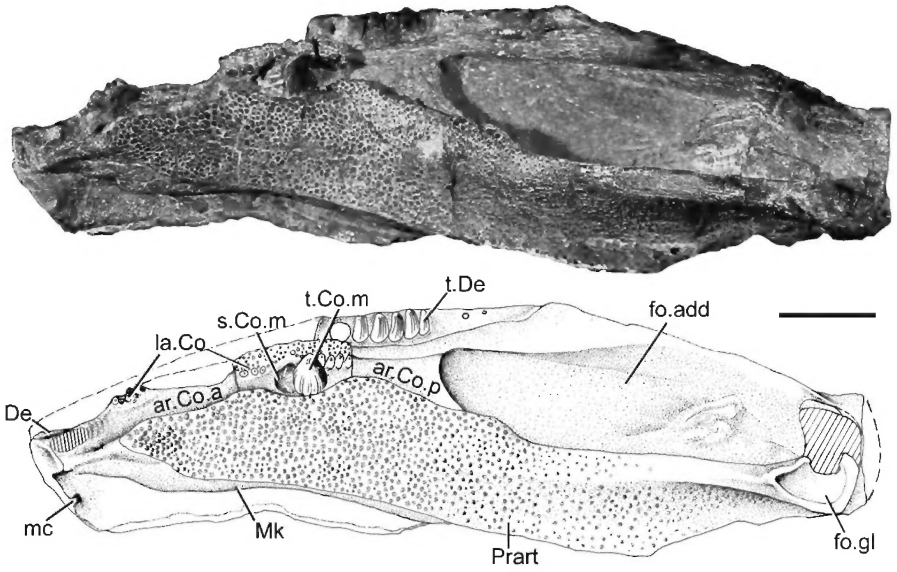

Fig. 3　The mandible of *Arquatichthys porosus* gen. et sp. nov. from Posongchong Formation, Lower Devonian, South China (holotype, IVPP V 15644) in lingual view

Abbreviations: ar. Co. a. anterior coronoid area; ar. Co. p. posterior coronoid area; De. dentary; fo. add. adductor fossa; fo. gl. glenoid fossa; la. Co. lateral portion of coronoids covered by small denticles; mc. mandibular sensory canal; Mk. Meckelian bone; Prart. prearticular; s. Co. m. socket for middle coronoid replacement tusk; t. Co. m. tusk of middle coronoid; t. De. marginal teeth of dentary; scale bar = 5 mm

The lingual side of the mandible shows a single, uniform tooth row on the dentary margin (Fig. 3). The attachment area for the parasymphysial dental plate is small, as in *Styloichthys*, *Youngolepis*, *Powichthys* (Jessen, 1980; Chang, 1991; Zhu and Yu, 2002, 2004). Its surface is broken in the anterior, however the preserved part, formed exclusively by the Meckelian bone, shows that the attachment area is arched presumably for the tooth whorl. In porolepiforms and onychodonts, the dentary forms a dermal anteromedial lamina as support of the parasymphysial tooth whorl (Ahlberg, 1992; Zhu and Schultze, 1997).

The anterior and the posterior coronoids are lost. The loose connection between coronoids and underlying Meckelian bone also occurred in *Achoania*, *Styloichthys*, and *P. thorsteinssoni* (Jessen, 1980; Zhu and Yu, 2004). The preserved middle coronoid holds a tusk and a pit. This tusk is slightly folded at the base similar to that in many "osteolepiforms" (Jessen, 1966; Schultze, 1970), and in *Kenichthys* (Chang and Zhu, 1993), *Youngolepis* and *Powichthys* (Jessen, 1980; Chang and Smith, 1992). The lateral portion of the coronoid bears numerous, randomly set, small denticles, similar to *Powichthys*, *Youngolepis*, *Kenichthys* and some "osteolepiforms" (*Medoevia* Lebedev, 1995). In many porolepiforms and some "osteolepiforms", this part bears only a single denticle row (Jarvik, 1980); in *Lamprotolepis verrucosa*, this part

bears two denticle rows (Vorobyeva, 1977). The prearticular is large, with shagreen of fine denticles. Its upper margin is uneven, similar to that in *Youngolepis* (Chang, 1991) and *Psarolepis* (Zhu and Yu, 2004). On the posterior end of the mandible, the prearticular stands at an angle to the dentary and infradentaries. An extensive anterior infradentary (splenial) flange is at the ventral margin of the mandible. This flange is present in *Powichthys*, *Youngolepis*, *Kenichthys* and porolepiforms, as well as in Middle Devonian "osteolepids" (Chang and Yu, 1997). The adductor fossa is large, occupying more than 40% of the mandible length.

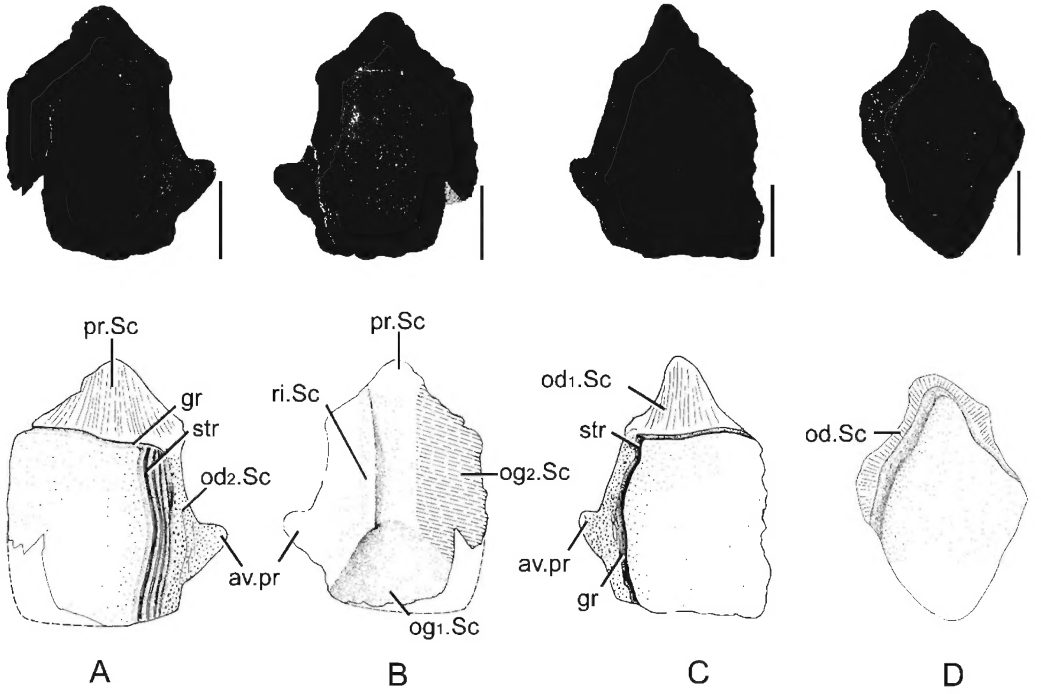

Fig. 4 *Arquatichthys porosus* gen. et sp. nov. from Posongchong Formation, Lower Devonian, South China
A–B. the flank scale, IVPP V 15645, dorsal and ventral views; C. the flank scale, IVPP V 15646, dorsal view; D. the dorsal-median scale, IVPP V 15647, dorsal view
Abbreviations: av. pr. anteroventral process; gr. groove separating overlapped and exposed areas; od, $od_{1,2}$. Sc. area overlapped by adjoining scales; $og_{1,2}$. Sc. area overlapping adjoining scales; pr. Sc. articular process of scale; ri. Sc. ridge on inner face of scale; str. striations paralleling to the groove at anterior margin of scale; scale bar = 1 mm

Scales: Several detached cosmine-covered scales have been collected from the same site. They are referred to *Arquatichthys porosus* for their cosmine pores are tiny and densely distributed as in the holotype. Their size is also compatible with that of the holotype. These scales are rhombic in shape and bear a strong anteroventral process. The same process is also observed in *P. spitsbergensis* (Clément and Janvier, 2004), *Youngolepis* and *Styloichthys* (Wang and Zhu, in prep.). It was mentioned that a much less pronounced anteroventral process is present in *Kenichthys*, *Thursius wudingensis* and *Youngolepis* from Vietnam (Clément and Janvier, 2004), however we fail to find such a process in *Thursius wudingensis*. The exposed cosmine area and its adjoining overlapped areas are separated by a groove. One to three distinct striations are parallel to the groove at the anterior margin, representing a unique feature of *Arquatichthys*. This striation zone is different from the narrow band of dentine tubercles in *Heimenia* (Ørvig, 1969; Jarvik, 1980; Wang, 1986), the band of tubercle-like units in *P. thorsteinssoni* (Clément and Janvier, 2004), and the short pectinate stripe area in *Porolepis* (Jarvik, 1980).

The internal surface of the scale is smooth. A visible low and narrow ridge is close to the anterior margin of the scale. This ridge is quite broad in *P. thorsteinssoni* (Jessen, 1980), straight and thin in *P. spitsbergensis* (Clément and Janvier, 2004). The socket is triangular and extensive, for articulating the peg of the scale next below and the anteroventral process of the adjacent scale.

4 Discussion

4.1 Phylogenetic position of *Arquatichthys*

Arquatichthys bears three coronoids. In this regard, it is phylogenetically crownward from *Psarolepis* and *Achoania* which possess five coronoids in addition to the parasymphysial tooth whorl (Zhu and Yu, 2004). The small attachment area for the parasymphysial tooth whorl, in combination with the L-shaped pit line of infradentary 4, identifies *Arquatichthys* as a basal dipnomorph (Jarvik, 1972; Jessen, 1980; Chang, 1991). However, the exact phylogenetic position of *Arquatichthys* can hardly be assured at present, and the further investigation reckons on new materials.

4.2 Possible sequence of scale character transitions among major sacropterygian groups

By mapping the scale features of *Arquatichthys* and other sarcoptergyian groups onto a simplified cladogram combined from Janvier (1996) and Zhu &Yu (2002), we suggest the following scale character transitions leading from basal osteichthyans to dipnomorphs and tetrapodomorphs (Fig. 5).

A developed anterodorsal process first appears in *Naxilepis*, a basal osteichthyan from Silurian (Wang and Dong, 1989). This process is common in actinopterygians such as *Moythomasia* and *Mimia* (Gardiner, 1984; Janvier, 1996; Schultze, 1992). The development of an anterodorsal process was considered as a scale morphocline from *Lophosteus* to *Cheirolepis* and *Howqualepis* or *Moythomasia* (Schultze, 1992). In some basal sarcopterygians, such as *Youngolepis* and *Styloichthys*, the developed anterodorsal process is still present (Wang and Zhu, in prep.). In addition, a new process,

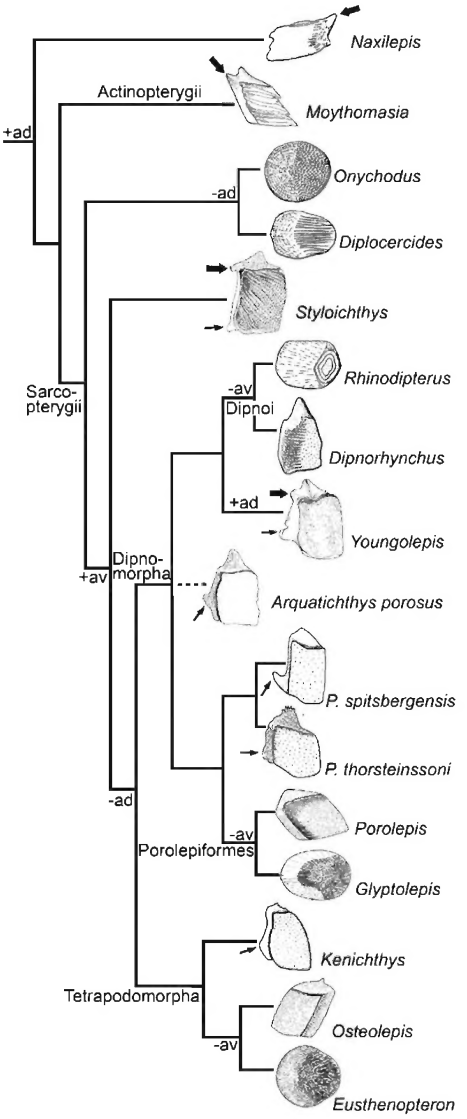

Fig. 5 Cladogram of major sarcopterygian groups (combined from Janvier (1996) and Zhu & Yu (2002)), showing a sequence of scale character transitions

The dotted line for *Arquatichthys* represents its unresolved phylogenetic position among dipnomorphs (*Naxilepis*, *Moythomasia*, *Onychodus*, *Diplocercides*, *Rhinodipterus* and *Dipnorhynchus*, from Janvier (1996); *P. spitsbergensis*, from Clément and Janvier (2004); *P. thorsteinssoni*, from Jessen (1980); *Porolepis*, *Glyptolepis*, *Osteolepis* and *Eusthenopteron*, from Jarvik (1980); *Kenichthys*, from Chang and Zhu (1993); *Styloichthys* and *Youngolepis*, from Wang and Zhu(in prep.))

Abbreviations: +ad. anterodoral process appears; +av. anteroventral process appears; -ad. anterodoral process disappears; -av. anteroventral process disappears

the anteroventral process, appears. The co-existence of two processes continues the sequence of scale character transitions from basal osteichthyans to basal sarcopterygians. Although the loss of these two processes is common in many sarcopterygians, the developed anteroventral process is present in *P. spitsbergensis* and *Arquatichthys*. The loss of these two processes in different sarcopterygian groups might represent a case of parallel evolution of scales, occurred in coelacanths, onychodonts, porolepiforms, lungfishes and most tetrapodomorphs (*Kenichthys* possesses a much less pronounced anteroventral process).

5 Conclusions

Arquatichthys porosus gen. et sp. nov., a new basal dipnomorph fish from the Pragian (Devonian) of China, is characterized by its highly arched mandible, elongate overlapped area on the mandible and several striations at the anterior margin of scale. The appearance of *Arquatichthys* provides useful information bearing on the evolution of basal dipnomorphs and on the early sarcopterygian divergence in the Early Devonian of China. The scales in *Styloichthys*, *Youngolepis*, *Arquatichthys* and *P. spitsbergensis* give a scenario of scale character transitions leading from basal osteichthyans to dipnomorphs and tetrapodomorphs. The exact phylogenetic position of *Arquatichthys* reckons on more materials in the future.

Acknowledgments We thank to Zhao Wenjin, Jia Liantao, Qiao Tuo and Geng Binghe (IVPP) for their assistance during field work, Xiong Cuihua for preparation, Huang Jinling for illustration. Thanks are also due to M. D. Brazeau (Uppsala University) for criticizing earlier versions of this manuscript.

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